

A Systematic Review of the Neotropical Ground-Cuckoos (Aves, *Neomorphus*)

by

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Introduction

Systematic studies of closely related species may elucidate the history of faunal differentiation within a given region. The direction of geographical character variation may allow one to reconstruct immigration paths; the occurrence of secondary contact zones may indicate the former existence of ecological barriers, although the barriers themselves may have long since disappeared.

I have chosen for this study the neotropical ground-cuckoos (*Neomorphus*) which are terrestrial birds restricted to the dark interior of Middle and South American forests. The pattern of speciation and distribution in these birds is of general zoogeographic significance, as these aspects are also characteristic of numerous other groups of interrelated South American forest species. Typical features are the occurrence of species with a restricted range in Amazonia despite the wide expanse of continuous forest and geographical exclusion of species in uniform environments, presumably as a result of ecological competition. Other interesting aspects of the distribution of the ground-cuckoos are the barrier effect of the lower Amazon River and the occurrence of two species in upper Amazonia inhabiting the lowlands and the Andean foothills, respectively.

1. The genus *Neomorphus*. — Ground-cuckoos are pheasant-like birds with a sharply ridged bill, strong legs, long tail, and a flat crest. They reach a length of about 50 cm and resemble in general appearance and mannerism the popular roadrunners (*Geococcyx*) of the southern United States and Mexico, where these birds inhabit arid scrub in non-forest areas. Four species of ground-cuckoos exist in the Neotropical Region. They differ in the color of the anterior under and upperparts as well as in the coloration of the bill and orbital skin (Table 1). The ground-cuckoos replace one another geographically and only one species inhabits a given forest region.

I group the four *Neomorphus*-species in two "zoogeographic species" (Mayr & Short 1970: 3), the *Neomorphus geoffroyi* superspecies and the *N. rufipennis* superspecies. If a broader concept would be applied, the genus might be combined with other related genera. In *Neomorphus* there is no sexual dimorphism in color, but males are larger than females.

2. Life history data. — Ground-cuckoos are uncommon birds that lead a secluded life on fairly open and well drained forest floor in hilly areas or broken terrain. Here they frequently follow army-ants to feed on disturbed insect prey, as do a number of antbirds (Formicariidae), wood-creepers (Dendrocolaptidae) and other forest birds. Ground-cuckoos also

eat lizards and other small animals and are said to follow bands of forest pigs (peccaries). Probably because of this habit and the conspicuous bill snapping which resembles the snapping of the jaws or tusks of peccaries, ground-cuckoos have been given vernacular names like "Pájaro Váquiro" in Venezuela (*N. rufipennis*) and "Mãe de porco" or "Jacú-Queixada" in eastern Brazil (*N. geoffroyi*; see Sick 1949: 234); "Tajaçú-uira", "Acanatic" (*N. g. geoffroyi*; see Snethlage 1914); "Sainero", the companion of wild pigs, in western Ecuador (*N. radiolus*).

Ground-cuckoos are difficult to detect in the shadows of the forest because of their bronze green or purple upperparts and patterned lower surface. The conspicuous blue or red, or blue-and-red bare orbital skin in the Amazonian forms may facilitate recognition in the dim light of their haunts. However, the bare postorbital skin is also bright blue and orange in the roadrunners (*Geococcyx*) of nonforest habitat. Like gallinaceous birds, ground-cuckoos walk or run swiftly and may hop occasionally to capture prey on the forest floor. When pausing they may raise the slightly spread tail somewhat above the horizontal. Ground-cuckoos sometimes perch a few feet high in the understory of the forest.

Vocalizations: When foraging and specially when disturbed, ground-cuckoos snap the strong mandibles. These snaps may be uttered in series to produce a loud crackling noise. Besides this mechanical sound several calls resembling those of forest doves have been reported (see species accounts below).

Nesting: Ground-cuckoos are nonparasitic and raise their own young. Sick (1949, 1962) in southeastern Brazil and E. O. Willis (pers. comm.) at Putuimi, eastern Ecuador, have observed pairs of *Neomorphus geoffroyi* each in company with, and caring for, one young bird. Juveniles are covered with blackish downy feathers and molt directly into subadult plumage. Sick (1949: 236) suspects that the nest may be built in thickets a few feet above the ground. The eggs of *N. rufipennis* are yellowish white and a sample of seven eggs measured 40.1×30.8 mm (Schönwetter 1964). Further aspects of the ground-cuckoos' breeding biology remain unknown.

Systematics and distribution

Ground-cuckoos inhabit forested areas of the Neotropical Region from Nicaragua to south-eastern Brazil and are found up to an elevation of about 1 000 m along the Andean foothills and the Central American mountains. They inhabit a variety of forest types ranging from good rain forest to semi-evergreen forests and montane woods. E. O. Willis (pers. comm.) found that *Neomorphus geoffroyi* preferred forest edges where antbird

competitors were less numerous. He therefore suspects competition with other antfollowing birds, including the forest falcon *Micrastur ruficollis* (!), may limit the distribution of this ground-cuckoo in some areas.

A survey of the four allopatric and parapatric ¹⁾ species comprising the genus *Neomorphus* with notes on distinguishing characters and details of their distribution is given in the following section (see also Table 1 and Fig. 1). Two species (*N. rufipennis*, *N. radiolus*) are monotypic and occupy rather restricted geographical ranges. The other two species, *N. pucheranii* and *N. geoffroyi*, are widespread and each has been subdivided taxonomically into two or more „subspecies“.

I share the current criticism of the subspecies concept where continuously distributed and clinally varying bird populations of large continental areas are concerned (Haffer 1974: 71; 1975: 50, 78). A typological subdivision of such populations into a series of „subspecies“ would obscure rather than clarify the nature of the geographical variation. Subspecies names should be used sparingly to label typical populations which originated in geographical isolation and are in secondary contact with other conspecific populations today. The subspecies concept also serves a useful purpose in classifying population samples of species with phenotypically distinct geographical isolates, e. g. in mountain or island regions (Mayr 1963: 349). In these cases „subspecies“ are sharply delimited and often phenotypically fairly uniform. I used subspecies names in the following review of the ground-cuckoos with the above qualifications in mind.

I collected the Rufous-vented Ground-Cuckoo in northwestern Colombia (Haffer 1975) and studied *Neomorphus* material in the museums of New York (AMNH), Philadelphia (ANSP), Pittsburgh (CM), Chicago (FMNH), Baton Rouge (LSU), Tring (BMNH), Berlin (Zool. Mus.), Bonn (Mus. Koenig), and Munich (Zool. Staatssammlung). Besides information taken from regional catalogues I also used data on ground-cuckoos contained in the following publications: Chapman (1917, 1923, 1926, 1928), Des Murs (1856), Deville (1851), Griscom & Greenway (1941), Gyldenstolpe (1945), Lehmann (1960), O'Neill (1974), Pinto (1962, 1964), Sick (1949, 1962), Snethlage (1927), Slud (1964), Todd (1925), Traylor (1958) and Wetmore (1968).

***Neomorphus geoffroyi* superspecies**

Neomorphus geoffroyi and *N. radiolus*

Characters. — Color of upper head and crest not uniform; breast feathers with dusky or black semicircular bands; orbital skin blue (except in adults of the trans-Andean population of *N. geoffroyi*).

Distribution. — Southern Amazonia, southeastern Brazil, foothills of Eastern Andes and trans-Andean region.

¹⁾ *Parapatric* species occur in non-overlapping geographical contact, with no or only very limited interbreeding. I use „parapatric“ for species which exclude each other geographically in ecologically uniform environments. Species that meet along sharp ecological breaks, such as forest/savanna, remain outside our discussion, although they also qualify as parapatric. *Allopatric* species also occupy mutually exclusive areas but are not in geographical contact. Therefore, the decision whether allopatric populations are still subspecies or have reached the level of species will remain highly subjective in many cases.



Fig. 1: Distribution of the *Neomorphus geoffroyi* species group.

Explanations: *Neomorphus geoffroyi* and *N. radiolosus* comprise the *N. geoffroyi* superspecies. *Neomorphus rufipennis* and *N. pucheranii* comprise the *N. rufipennis* superspecies. Symbols indicate collecting localities. Shaded areas — *N. geoffroyi*. Uniform gray shading — *geoffroyi* subspecies group: Closed stars — *N. g. geoffroyi*. Open stars — *N. g. australis*. Open stars in black circles — *N. g. squamiger*. Semiclosed triangles — *N. g. maximiliani*. Semiclosed squares — *N. g. dulcis*. Shaded by vertical hatching — *salvini* subspecies group: Open squares on edge — *N. g. aequatorialis*. Open squares — *N. g. salvini*. Area dashed horizontally and open triangles — *N. radiolosus*. Area stippled and closed circles — *N. rufipennis*. Area

Neomorphus geoffroyi (Temminck, 1820)

Rufous-vented Ground-Cuckoo

Coccyzus geoffroyi Temminck, Planch. Col., livr. 2, 1820, pl. 7 (no locality; vicinity of Pará, Brazil, Peters 1940, p. 62).

Illustrations. — Temminck 1820, Planch. Col., livr. 2, pl. 7 (*N. g. geoffroyi*); Sick 1949, p. 232—233 (*N. g. dulcis*); Pinto 1964, opposite p. 176 (*N. g. dulcis*); Sclater, Proc. Zool. Soc. London 1866, pl. 5 (*N. g. salvini*); Davis, Birds Mexico and Centr. America, Univ. Texas Press, pl. 12 (*N. g. salvini*); Wetmore, 1968, p. 142 (*N. g. salvini*).

Characters. — Upperparts metallic green to bronze purple, crest bluish black. Underparts grayish or buffy, pectoral band black, abdomen chestnut. Bare skin behind eye bright blue in cis-Andean populations but neutral or dark gray in adults of trans-Andean *N. g. salvini*; juveniles of the latter form still have a large bright blue spot on the temporal area (see below).

Two distinct subspecies groups ("megasubspecies" Amadon & Short 1976) may be distinguished on the basis of crown and breast color, as follow:

Geoffroyi group: *N. g. geoffroyi*, *squamiger*, *australis*; *maximiliani*, *dulcis*¹⁾. Forehead and crown barred or mottled (rufous-buffy brown and bluish black or dark greenish brown with paler feather margins). Breast feathers with conspicuous dusky semicircular bands. This bold squamation varies considerably in extent in the nominate form and is reduced in *N. g. australis* with a nearly plain central chest. Weight of three adult males of *N. g. dulcis* 339—355 (349) gr, one female 349 gr (Sick 1949).

Salvini group: *N. g. salvini*; *aequatorialis*. Forehead and crown uniform cinnamon-brown (*salvini*) or warm brown (*aequatorialis*). Breast feathers with broad pale tips, the dusky semicircular bands being only faintly indicated.

It is not known whether the *geoffroyi* and *salvini* subspecies groups meet in eastern Peru. No specimens have been collected in the potential contact area in the hills east of the upper Ucayali Valley (Fig. 1). I have

¹⁾ In this and the following lists of subspecies, a comma separates clinal subspecies and a semicolon separates geographically isolated forms.

Fig. 1, Explanations, cont.:

hatched horizontally — *N. pucheranii*; Open circles — *N. p. pucheranii*. Semiclosed circles — *N. p. lepidophanes*.

Andes mountains above 2000 m elevation are in black. Diagrams illustrate the species of ground-cuckoos. Lateral breast feathers depict geographic variation in color pattern. Observe semicircular bands on breast feathers in *N. geoffroyi* and *N. radiolus*, but black apical margins of these feathers in *N. rufipennis* and *N. pucheranii*.

no doubt that *N. g. geoffroyi* and *N. g. aequatorialis* would hybridize extensively if in contact in this area.

Juvenal plumage. — The juvenal plumage of the ground-cuckoos is remarkable because of its blackish coloration (Sick 1949: 231). T. Howell (1957) collected in Nicaragua a juvenal female of *N. g. salvini* not far beyond the nestling stage and permitted me to quote from his unpublished description of this bird (only brief notes on the nestling of *N. pucheranii* have been published previously, Shelley 1891: 418): "The entire plumage is heavily pigmented and at a distance appears black. In a few areas that are pale brownish in the adult some traces of this color are present. In the following description all mention of green, bronze, and purple refers to a gloss of these colors on essentially black feathers. Body feathers downy, deep brownish black, more blackish on back and breast, becoming paler and more brownish on the abdomen. The feathers of the back are faintly bronze terminally and faintly purple subterminally. Feathers on the coronal area are elongate and form a crest which extends back to the nape. These feathers are bronze or bronze green narrowly tipped with purple. The pre-ocular feathers are wholly or partly light grayish brown.

Inner web of feathers of alula purplish black, outer web dull bronze green, becoming purplish black near the shaft on proximal half.

Secondary coverts green basally, then purple, then bronze crossed with narrow bands of purple. Secondaries green, tipped with subterminal bands of purple and terminal bands of bronze. Primaries much duller, indistinctly glossed with green and purple. Rectrices similar to secondaries — green for basal two thirds, then a broad band of purple, a narrower tip of bronze. Color of soft parts: The lining of the mouth was rose pink, with small white rugosities in the maxillo-palatine region. The iris was dark brown. The legs and feet were light blue-gray or plumbeous; in the dried skin they have become horn color. The bill was black. The orbital skin was deep charcoal gray with the exception of a *bright blue spot on the bare temporal area* about 5 mm posterior to the eye. The blue area has not kept its color, but the dried skin is still largely blackish."

Vocalizations. — Loud snapping of the mandibles. A mournful call (*hooh*) like that of the Juruti doves (*Leptotila rufaxilla* and *L. verreauxi*) has been reported by Natterer (in Pelzeln 1868). E. O. Willis (pers. comm.) also heard a low *coo* or moan from *N. geoffroyi*. The Indians of the Balta region, eastern Peru, described a call of this cuckoo "as a prolonged, rising hum" (O'Neill 1974). Slud (1964: 129) heard from *N. g. salvini* in Costa Rica a "low muffled 'woof' or 'woofwoof woof', like wing rustling of a vulture or the hum of a distant motorboat". Wetmore (1968) heard "a low croaking note" in Panamá.

Geographical variation and population structure. — Two sharply distinguished groups of populations (subspecies groups) may be recognized: The *geoffroyi* group of southern Amazonia (*geoffroyi* — *squamiger* — *australis*) and southeastern Brazil (*maximiliani* — *dulcis*) forms widespread and clinally varying populations in the two respective distribution areas. The *salvini* group is comprised of two geographically isolated populations occupying the eastern Andean foothill zone in upper

Amazonia (*aequatorialis*) and hilly areas in southern Middle America to northwestern Colombia (*salvini*), respectively (Fig. 1).

Neomorphus g. geoffroyi group: Color characters vary mostly clinally. The upperparts are olive green in Pará (*g. geoffroyi*); this color intensifies in SE Brazil from dark impure bronze green in Bahia (*g. maximiliani*) to dark blue in Espírito Santo (*g. dulcis*). The color of the abdomen also darkens in the same direction (Snethlage 1927, Pinto 1962, 1964).

Very little material is available from central Brazil where Sick (pers. comm.) observed this species along the upper Rio Xingú (X of Fig. 1). Snethlage (1927) compared a specimen from the Rio Manoel Correa, Mato Grosso (not located and not shown on Fig. 1); because of its bronze green back this bird agrees with typical *g. geoffroyi* from Maranhão. I also refer the population near Peixe, upper Rio Tocantins (P of Fig. 1; Pinto 1964) to the nominate subspecies, although no material appears to be available from this area. The specimen from the "Rio Araguaya", Goiás, mentioned by Deville (1851: 212) and described by Des Murs (1856: 22), probably was also an example of *N. g. geoffroyi*; the exact collecting locality along the Araguaya River, however, is unknown.

Hellmayr (1910) found four specimens from the upper Rio Madeira region (Calamá, Maruins) to resemble closely birds from Pará (*N. g. geoffroyi*). I have examined these specimens which are preserved in New York and Munich and agree with Hellmayr.

Neomorphus geoffroyi was unknown from the upper Amazonian lowlands west of the Rio Madeira, until O'Neill (1974) reported a pair from Balta, eastern Perú, in the headwater region of the Rio Purús (B of Fig. 1). This area receives somewhat less rainfall than the upper Madeira region and is covered with Dry Tropical Forest (Tosi 1960, Haffer 1969, 1974: Fig. 5.4). In response to these environmental conditions, the plumage color of the Balta specimens is somewhat paler than that of specimens of typical *N. g. geoffroyi* collected farther east (Madeira Valley, Belém region). The abdomen and flanks are less rufescent in the Balta specimens, the lower breast and belly are somewhat paler as is the rufous barring of the forehead and crown. The markings of the breast are less developed, especially in the male, the feathers of the central portion of the lower breast being almost plain or showing only a small spot or short streak along the shaft (similar to *N. g. australis*). The concentric bands are somewhat more conspicuously developed in the female, indicating pronounced individual variation in this character as is also the case in populations of eastern Brazil. The color of the upper back is bright olive as in the nominate form. The Balta population probably occupies a position in a cline from typical *g. geoffroyi* of central and northern Brazil to *N. g. australis* of eastern Bolivia.

The *geoffroyi* and *salvini* groups of *N. geoffroyi* may not be in contact in eastern Perú, where the valley of the upper Río Ucayali and the savanna country of the Gran Pajonal separate *N. g. aequatorialis* (ranging along the Andean foothill zone south to the upper Pachitea Valley) from *N. g. geoffroyi* which inhabits the hill country to the east. However, more field observations and collecting are needed to ascertain the distribution of these cuckoos in southeastern Peru.

Neomorphus g. australis is clinally related to *N. g. geoffroyi* and comprises the populations inhabiting the Andean foothills of southeastern Peru and eastern Bolivia. The coloration of specimens from these populations differs in narrower barring of forehead, crown and sides of the face, and by almost plain light gray throat and central breast, where markings are conspicuously reduced. The median breast feathers have only narrow dusky margins, the concentric bands being very faint. By contrast, the concentric bands on the lateral breast feathers are dusky and conspicuous. The color of throat and belly varies individually in intensity (very light to pale gray) as does the width of the pectoral band which is rather narrow and almost broken centrally in two specimens (Bond 1955). The type of *N. g. australis* from Huanay is boldly marked on the lateral breast feathers, a character which is also subject to individual variation.

Birds from the valley of the lower Rio Tapajós as well as from the southern bank of the Amazon River west and east of the mouth of the Tapajós (Pará, Brazil; *N. g. squamiger*) have an indistinct black pectoral band which is lacking in some specimens collected near the Amazon (e. g. Parintins and Cussarí). The forehead and crown are covered with brownish or dark greenish feathers with paler, buffy to whitish, margins and tips or by buffy brown feathers tipped dull bluish and with bluish centers. Although described as a separate species, Peters (1940) stated that *squamiger* is probably conspecific with *N. geoffroyi*. However, he considered *squamiger* distinct because of incomplete knowledge of the distribution of both forms. Meanwhile Griscom et al. (1941: 155) described additional specimens of *squamiger* which show an approach to *geoffroyi*, as they have a fairly distinct pectoral band and buffy brown feathers of the crown tipped bluish and with bluish centers ¹⁾.

Two specimens from Cussarí, on the south bank of the Amazon and east of the mouth of the Rio Tapajós, had been referred to *N. g. geoffroyi* by

¹⁾ Griscom et al. (1941: 154) separated an additional subspecies, *N. g. iungens*, which Gyldenstolpe (1945: 63) showed to be invalid. One possible reason for Griscom et al. (l. c.) describing their birds as different from *N. g. squamiger* may have been their erroneous impression that in *squamiger* "the forehead and pileum are mostly bluish like the crest" (l. c.: 156). This and other misleading statements render their review of *Neomorphus* inaccurate in certain details.

Sneath (1914) before Todd (1925) described *N. squamiger*. These birds are preserved in the Berlin museum where I examined one skin and in the Goeldi Museum (Belém; Dr. F. C. Novaes, pers. comm.). The population at Cussarí is not *N. g. geoffroyi*, as a black pectoral band is lacking. The sides of the head are uniform buff and the crest is blueblack in the Berlin specimen. I refer the Cussarí population to *N. g. squamiger* instead. Meyer de Schauensee's argument (1966: 140) in favor of the specific distinctness of *squamiger* and *geoffroyi* was based on his erroneous assumption that the population at Cussarí represents *N. g. geoffroyi*; the argument is thus no longer valid. Additional material presently available indicates the close relationship of *g. geoffroyi* and *squamiger* which I consider to be conspecific. Specimens from the upper Tapajós Valley, from the Xingú and the lower Madeira Rivers are needed to prove a smooth intergradation of both forms.

Neomorphus g. salvini group: Despite the large gap between the distribution areas of *N. g. salvini* and *N. g. aequatorialis*, these subspecies are similar in the uniform brown color of the forehead and crown and in the color of the breast feathers, which are tipped pale (Table 1). *N. g. aequatorialis* comprises populations inhabiting the Andean foothill forests from eastern Perú north to southeastern Colombia. The main color characters, i. e. warm brown forehead and crown as well as obscure markings of the breast feathers, are fairly constant in the examples collected so far. A female bird from Puerto Victoria on the Río Pachitea, eastern Perú (Museum Koenig, Bonn) has the front and the eye "brows" narrowly barred. Faint indications of similar barring also occur in other specimens of *N. g. aequatorialis* from different portions of the range and probably are due to individual variation rather than introgression of *N. g. geoffroyi* genes.

The populations of *N. g. salvini* (forehead and crown cinnamon brown) vary somewhat clinally. Birds from northwestern Colombia have a less rufescent crown than specimens from Nicaragua, thus showing an approach toward *N. g. aequatorialis* (see Chapman 1923). A female from Quimarí in the upper Sinú region of northwestern Colombia "is paler below than a pair from Juradó on the Pacific coast and the terminal pale spots on the feathers of the upper breast are whiter and more conspicuous" (Meyer de Schauensee 1950: 121).

Distribution. — The Rufous-vented Ground-Cuckoo inhabits forests of southeastern and central Brazil south of the Amazon River, along the eastern Andean foothills of Bolivia, Perú, Ecuador, and southeastern Colombia (Fig. 1). It also occurs west of the Andes from the Baudó Mountains of Pacific Colombia through Panamá and Caribbean Costa Rica to Nicaragua, where it is found locally in the Tropical and lower Subtropical

Zone. The published locality records are listed in more detail below (a reference is given only for recent records not included in one of the standard catalogues):

Neomorphus g. geoffroyi group.

1. *Neomorphus g. geoffroyi* (Temminck, 1820). — Brazil, Pará: Vicinity of Pará (= Belém; type locality)¹⁾; Maivari and Barra near Belém (Pelzeln 1870)²⁾; Igarapé Assú; Santo Antonio do Prata; Rio Capim; Baião (Rio Tocantins; AMNH); Pimental; Rio Gurupi (Paragominas, Pará; Novaes, pers. comm.); Cussary; Amazonas: Calamá (Rio Madeira); Maruins (Rio Gi-Paraná, Zool. Samml. Munich). Goiás: "Rio Araguaya"; Peixe (Pinto 1964); Maranhão: Turiassú (type locality of *N. g. "amazonicus"* Pinto, 1964); Mato Grosso: Rio Manoel Correia; Diauarum (upper Rio Xingú, sight record, H. Sick, pers. comm.). Perú: Balta, Dep. Loreto (O'Neill 1974, *g. geoffroyi* \geq *australis*).

2. *Neomorphus g. squamiger* Todd, 1925. — Brazil, Pará: Santarém (Colonia do Mojui, type locality); Diamantino near Santarém (E. O. Willis, pers. comm.); Tauary; Piquiatuba; Caxiricatuba; Prainha; all localities on the right bank of the lower Rio Tapajós; Patinga; Boim; Morro do Pau da Letra; Villa Braga (Goeldi Mus., Dr. F. Novaes, pers. comm.) on the left bank of the Tapajós River. Amazonas: Cussari (Mus. Goeldi, Belém); Villa Bella Imperatriz (= Parintins; AMNH). Records of *N. "squamiger iungens"* Griscom et al. (1941) are here included under *N. g. squamiger* for reasons outlined in the text above.

3. *Neomorphus g. australis* Carriker, 1935. — Bolivia, Dep. La Paz: Huanay, 1500 feet, Rio Mapirí (type locality); Santa Ana on the Río Coroico. Perú, Dep. Puno: Huacamayo (Bond 1955: 235); Dep. Madre de Diós: Boca Colorado (FMNH); Manu National Park, near Cashu Cocha (Terborgh & Weske, observ.); Dep. Cuzco:

¹⁾ I follow Snethlage (1927), Peters (1940), Griscom et al. (1941), and Pinto (1962) who established that Temminck (1820) had used a specimen from the Belém region for his original description and illustration of *N. geoffroyi*. The vicinity of Belém thus becomes the restricted type locality of the nominate subspecies. Hellmayr stated in a letter to J. L. Peters (Sept. 9, 1936; archives of the Mus. Comp. Zool., Cambridge, Mass.; Dr. R. Paynter, pers. comm.) "that the Pará birds agree precisely with plate 7 in the "Nouveau Recueil" of Temminck ... The nomenclature thus seems settled, whether the Paris or Leiden specimen be the real type. Both probably were from the same source, as the one in Leiden is said to have been received from the Paris Museum". Pinto reversed his previously published opinion (1962) in his later book (1964) the text of which, however, may have been written earlier than his 1962-article. Pinto (1964) accepted Bahía as the terra typica of *N. g. geoffroyi* and described the population inhabiting Pará, Mato Grosso and the Madeira region under the proposed new name *N. g. "amazonicus"* subsp. nov. I consider this name a synonym of *N. g. geoffroyi*.

²⁾ J. Natterer collected *N. geoffroyi* in "Pará in the forest along the trail to Maivari ..., and trail to Barra ..." (Pelzeln 1870: 271; translated from German). It is clear from this statement and has been confirmed by Dr. F. C. Novaes (pers. comm.) that both Maivari and Barra are localities near Belém. "Barra" in this context does not refer to "Barra do Rio Negro" (= Manaus) on the north bank of the middle Amazon, as Pinto (1964: 177; under synonymy of "*N. g. amazonicus*") tacitly assumed. The "Camino da Barra" passed by Val-de-Cans and ended opposite Isla da Barra, about 10 km north of Belém (Dr. Novaes, pers. comm.). Maivari (Maguary, Magoari) is located about 12 miles to the northeast of Belém. *Neomorphus geoffroyi* has long disappeared from the forests around the city of Belém, as later ornithologists have not encountered it in this region.

Quincemil (FMNH); Marcapata Valley, Hacienda Cadena (Peabody Mus., Yale Univ.).

4. *Neomorphus g. maximiliani* Pinto, 1962. — Brazil, Bahia: Rio Gongogy (type locality); Nazaré; Rio Jagoaripe; Rio Belmonte (= Rio Jequitinhonda).

5. *Neomorphus g. dulcis* Snethlage, 1927. — Brazil, Espírito Santo: Lagoa Juparaná (type locality); Linhares (Mus. Bonn); Mutum do Norte and Rio São José (Mus. Bonn, Sick 1949); Baixo, Guandú (AMNH); Minas Gerais: Teófilo Ottoni (AMNH); Rio Sussui; Rio Matipó; Rio Doce; Rio de Janeiro: Cantagallo.

Neomorphus g. salvini group.

6. *Neomorphus g. aequatorialis* Chapman, 1923. — Perú, Dep. Huánuco: Fundo Sinchona and Divisoria in the Cordillera Azul, LSU and FMNH, Traylor 1958); Dep. Pasco: Puerto Victoria (Mus. Bonn); Cacazú, 3000 feet; and Yurinaqui Alto, 3000 feet (FMNH). Ecuador: Huilca, 4000 feet (type locality); Rio Copotaza; Rio Suno; San José de Sumarco; Limoncocha (LSU); Río Lagartococha (AMNH). Southeastern Colombia: Included in range by Meyer de Schauensee (1966, 1970), although specimens have not yet been collected in this country. E. O. Willis (pers. comm.) observed this species at Umbria, Dep. Putumayo, and near Paraiso, above Florencia, Dep. Cármeta, in the Andean foothill zone.

7. *Neomorphus g. salvini* Sclater, 1866. — Northwestern Colombia: Juradó; Río Tanela; Villa Arteaga (Wetmore 1968); Alto Bonito (1500 feet); Alto del Buey in Baudó Mountains (3500 feet); Quimari; Tucurá on upper Río Sinú; upper Río Verde; and upper Río San Juan northeast of Turbo (last three records E. O. Willis observ., pers. comm.). Panamá: Santiago (Veraguas, type locality); Río Calovevora; Cordillera de Tolé; Barro Colorado and Gatún (Canal Zone); Cerro Campana (E. O. Willis, pers. comm.); Chilar (Colón); Cerro Chucantí; Charco del Toro; Cerro Pirre; Cana; Río Tuquesa; Cerro Tacarcuna; Tapalisa; Cituro (Darién); Permé; Armila; Puerto Obaldía (San Blas). Costa Rica: Río Reventazón (2000 feet); Sixaola; Río Sarapiquí; Miravalles; La Vijagua; Cerro de Santa María; Bonilla; Hacienda Volcan Turrialba; Hacienda La Iberia; Río Estrella (BMNH). Nicaragua: "Dep. Chontales" (vicinity of La Libertad or Santo Domingo); Savala; Río Tumo; Peña Blanca; San Emilio; El Recreo; 25 km south of Raspam.

Species limits. —The Rufous-vented Ground-Cuckoo may be in contact with *Neomorphus pucheranii* in the upper Amazonian lowland forests of eastern Ecuador — Perú — western Brazil (Fig. 1). Present evidence indicates that these two species are parapatric. I assume they exclude each other geographically as a result of ecological competition. *N. g. geoffroyi* and *N. pucheranii lepidophanes* occupy the same type of lowland forest in western Brazil and eastern Perú, although the middle and lower Río Purús may hinder a broad contact. These forms should meet, however, in the upper Río Juruá region. In eastern Ecuador, *N. geoffroyi aequatorialis* may be restricted to the Andean foothill region and *N. p. pucheranii* may be confined to the level lowlands at some distance from the Andes mountains; both species possibly established contact in the transition zone from foothills to lowlands.

The broad lower Amazon River limits the northward dispersal of *N. geoffroyi*, thus preventing a geographical contact of this species with *N. rufipennis* of the hilly interior of the Guianas and southern Venezuela.

In western Colombia, *N. geoffroyi salvini* is separated from *N. radiolus* by the flat and swampy Atrato and San Juan River valleys which both species avoid. They may be in contact in the Pacific foothills of the Western Andes of Colombia.

Neomorphus radiolus Sclater & Salvin, 1878

Banded Ground-Cuckoo.

Neomorphus radiolus Sclater & Salvin, Proc. Zool. Soc. London 1878, p. 438, pl. 27 ("Intaj" = Intac, NW Ecuador).

Illustrations. — Sclater & Salvin 1878, pl. 27; Meyer de Schauensee 1964, pl. 3; 1970, pl. 44 (head only).

Characters. Underparts banded black and buffy white; forehead and lower mantle blackish, barred buffy white; crown, crest, hind neck and upper mantle blue black; wings and lower back maroon; central rectrices metallic green, the rest deep purple green. Bare orbital skin, as recorded on specimen labels of two Colombian females, "blue to back of head" (Jimenez) and "light blue" (Río Mechengue) and, a Colombian male, "bluish violet" (La Costa).

Geographical variation and population structure. — Monotypic species. Only a dozen or so specimens of this rare and geographically restricted ground-cuckoo have reached various museums and little is known on geographical variation (Meyer de Schauensee 1948—1952: 495; Lehmann 1960: 268). The species is probably comprised of a series of continuous populations along the wet Pacific foothill zone of the Ecuadorian and Colombian Andes. The typical black pectoral band of *Neomorphus* is usually indistinct on the blackish underparts of *N. radiolus*, but fairly well defined in some specimens from northwestern Ecuador (Chapman 1926, Blake 1936).

Distribution. — Foothill zone (500—1 200 m elevation) of the Cordillera Occidental of northwestern Ecuador and western Colombia ranging from Guala north at least to the hinterland of Buenaventura and possibly beyond to the headwater region of the Río San Juan (Fig. 1).

Individual locality records follow (Chapman 1926, Meyer de Schauensee 1948—1952): Northwestern Ecuador: Intac (type locality); Paramba; Montes de Achotal (15 km south of Paramba; FMNH); Guala; Río Cayapas (AMNH). Western Colombia: Río Mechengue (720 m); La Costa (1000 m); above Jimenez (900 m; AMNH¹).

¹) M. G. Palmer collected birds above Jimenez, a village east of Buenaventura and obtained a female of *N. radiolus* unreported by Hellmayr (1911) and Chapman (1917). Jimenez (1600 feet above sea level) is located "a morning's walk from Los Mangos (= Cisneros or Juntas, Río Dagua), in a deep ravine by the side of the pass between Los Mangos and a place called Ventanas ..." in heavily forested country (Hellmayr 1911).

Species limits. — *Neomorphus radiolus* avoids the level Pacific lowlands of northwestern Ecuador and western Colombia resembling, in this respect, its northern representative *N. geoffroyi salvini*. Both species may be in contact in the headwater region of the Río Atrato and Río San Juan; however, no specimens are at hand from this area to substantiate our assumption. *N. radiolus* and *N. geoffroyi* are probably so similar ecologically as to be unable to occupy the same forest and therefore, if in contact, exclude each other geographically as a result of ecological competition.

***Neomorphus rufipennis* superspecies**

Neomorphus rufipennis and *N. pucheranii*

Characters. — Upper head and crest uniform blue black; breast feathers margined apically with black or blueblack. Orbital skin red and blue or entirely red.

Distribution. — Upper Amazonia, southern Venezuela and Guyana.

Neomorphus rufipennis (G. R. Gray, 1849)

Rufous-winged Ground-Cuckoo

Cultrides rufipennis G. R. Gray, Proc Zool. Soc. London 1849, p. 63, pl. 10 ("Supposed to be a native of Mexico", error = lower Orinoco River region, Venezuela).

Neomorphus nigrogularis Chapman, Bull. Amer. Mus. Nat. Hist. 33, 1914, p. 194 (Mt. Duida, SW Venezuela, 700 feet).

Illustrations. — Gray, Proc. Zool. Soc. London 1849, pl. 10; Chubb, Birds of British Guiana, vol. 1, 1916, pl. 9.

Characters. — Upper head, crest, neck and upper breast deep purplish blue, throat ashy. Rest of underparts pale ashy, dusky on undertail coverts. Back olive, central rectrices metallic purple, rest greenish black. Bare facial skin red.

Vocalizations. — Loud snapping of the mandibles, given singly or in pairs. P. Schwartz (pers. comm.) reported on this cuckoo's vocalization (Fig. 2) as follows: "The call is given singly and repeatedly at fairly frequent intervals but with no recognizable cadence or pattern. It is very like the hoot of some pigeon or owl: "whóu". The cuckoo's call is rather similar to that of the Blue Ground-Dove, *Claravis pretiosa*, but is a little longer and with a strong pitch accent at or near the beginning, which is mostly one of frequency and only slightly of amplitude."

Geographical variation and population structure. — Monotypic species. Probably forms interconnected populations in the foothill zone of the mountains of southern Venezuela, Guayana and north-

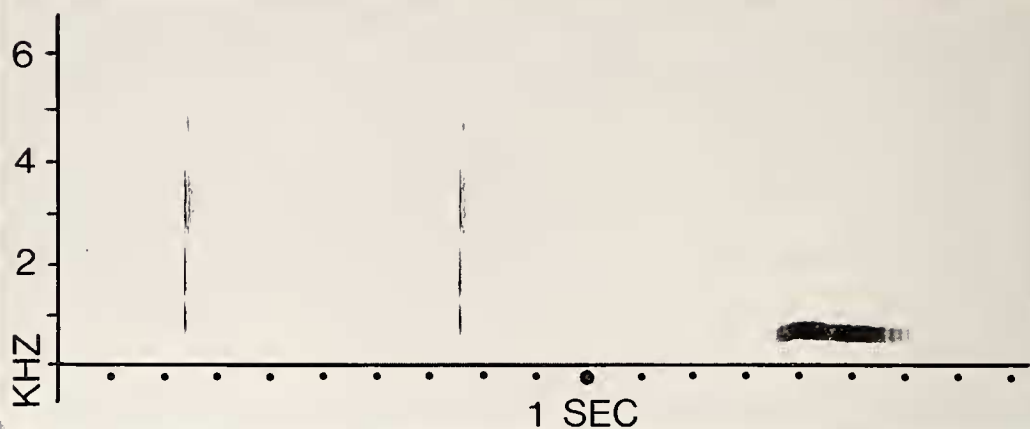


Fig. 2: Sonagrams of vocalizations by the Rufous-winged Ground-Cuckoo (*Neomorphus rufipennis*).

Left — two bill snaps. Right — call *whóu*. Río Grande, east of El Palmar, northeastern Dep. Bolívar, southern Venezuela. Recordings and sonagrams (wide band) by Paul Schwartz.

ernmost Brazil. The throat color varies in specimens from the range of *N. rufipennis* from ashy white to dark gray. I agree with Phelps & Phelps (1958: 153) who synonymized *N. nigrogularis* with *N. rufipennis*. Peters (1940) had considered them as valid geographical subspecies.

Distribution. — Restricted to the highlands of southern Venezuela and western Guyana, where it inhabits the foothill zone of the mountains (200—1000 m); also found around Mt. Arimaní in the upper Río Branco Valley, Dep. Roraima, northern Brazil.

Individual records are listed below (Phelps et al. 1958, Snyder 1966): Venezuela: Nuria; Río Grande (east of El Palmar, Dep. Bolívar; P. Schwartz, pers. comm.); Kabanayén; Cerro Auyántepeui; Caño Antabari; Suapure; "lower Caura River"; Cerro El Negro; Caño Cataniapo; Caño Cuao; Las Carmelitas; Mt. Duida. Guyana: Ituribisi River; Supenaam River; Mazaruni River; Kamakusa; Amai; Bartica, Cuyuni River (BMNH); Arawai River (BMNH); "Demerara" (BMNH). Brazil: Mt. Arimaní (upper Río Branco; Pelzeln 1871).

Species limits. — *Neomorphus rufipennis* is restricted to the forests of the mountainous region of interior northern South America. Since this species does not enter the adjoining Amazonian lowland forests, it did not establish contact with other ground-cuckoos. A potential contact zone between *N. rufipennis* and *N. pucheranii* exists in the upper Río Negro region, although no specimens are available from that area. A wide gap separates *N. rufipennis* and *N. geoffroyi*, the latter species being held back by the broad lower Amazon River. Considering the degree of difference in plumage color of *N. geoffroyi* and *N. rufipennis* I doubt that these species would hybridize if they were in contact.

Neomorphus pucheranii (Deville), 1851

Red-billed Ground-Cuckoo

Cultrides Pucheranii Deville, Rev. et Mag. Zool. 14, 1851, p. 211 ("L'Ucayale et l'Amazon" = Río Yaguas, northeastern Perú; Peters 1940, p. 63).

Neomorphus napensis Chapman, Amer. Mus. Novitates 332, 1928, p. 5 (Junction of the Río Curaray with the Río Napo, northeastern Perú).

Illustrations. — Des Murs 1856, pl. 7 (*N. p. pucheranii*), pl. 6 (*N. p. lepidophanes*).

Characters. — Forehead, crown and crest uniform dark glossy blue; forehead in some specimens (probably subadult) brown; breast feathers faintly (*p. pucheranii*) or boldly margined apically with black (*p. lepidophanes*) giving a squamate effect. Bill red, tip green or yellow; orbital skin red and blue (see below). Breast and belly light gray in *p. pucheranii* and clay color in *lepidophanes*; upperparts green with bronze tinge, primaries violaceous blue, tail dark green and violaceous.

The plumage of the nestling resembles that of *N. geoffroyi* (see above) and is blackish to dark brown, "passing into glossy olive green on the crest, which is fully developed; primaries and tail glossed with purple; secondaries partially washed with chestnut" (Shelley 1891). An immature male from Yucabí, upper Rio Negro (AMNH) is molting from juvenal to subadult plumage. Certain aspects of the coloration like the clay-colored belly and abdomen and the conspicuous black apical band of the breast feathers resemble color characters of adults of *N. p. lepidophanes* of the forest region south of the Solimões. However, these characters as well as the brownish forehead probably are typical only of subadult birds of *N. p. pucheranii*.

Vocalizations. — Bill snapping as in other ground-cuckoos. A "curious roaring noise" resembling the hum of a curassow (*Crax* sp.) has been reported by Olalla for *N. p. lepidophanes* of the upper Juruá Valley (Gyldenstolpe 1945).

Geographical variation and population structure. — Two subspecies. The populations north of the Solimões-Marañón River are characterized by a fairly uniform ashy breast and abdomen (*p. pucheranii*), whereas all birds collected south of this river are clay color below and their breast feathers are conspicuously margined with black (*p. lepidophanes*). The Solimões River itself seems to be the boundary between these phenotypically different populations ("subspecies"). The bare orbital skin is described as "eyelids and temporal arc blood red, the bare area on both sides of the head cerulean blue" for the type of *p. lepidophanes* from the lower Rio Purús (Todd 1925). Des Murs' illustration (1856, pl. 7) of the type of *p. pucheranii* from Santa Maria north of the Solimões also shows

a patch of dark blue skin behind the eye. This is confirmed by Hauxwell who collected a pair of *p. pucheranii* at Pebas, Peru and stated on the specimen labels (BMNH): "... skin around the eyes red, skin behind the eye light blue double winged".

Distribution. — Upper Amazonian lowlands north and south of the Rio Solimões-Marañón, reaching the Rio Purús in the south and the upper Rio Negro in the north.

Individual locality records are listed below:

N. p. pucheranii (Deville), 1851. — Perú: Santa María de las Yaguas, Río Yaguas (type locality)¹; Pebas; mouth of Río Curaray. Brazil: Tonantins on the Rio Solimões (CM); Yucabí on the upper Rio Negro (1 imm., AMNH).

N. p. lepidophanes Todd, 1925. — Brazil: Nova Olinda (type locality) and Hyutanahan on the Rio Purús (CM); Igarapé do Gordão and João Pessoa on the Rio Juruá (Riksmuseets Stockholm); São Paulo de Olivença on the Rio Solimões (CM). Perú: Orosa on the Rio Solimões (AMNH); "L'Ucayale" (= lower Río Ucayali, Deville 1851; no definite locality given and therefore not marked on our map, Fig. 1); San Fernando on the Rio Yavarí (1 ♂, FMNH).

Species limits. — *N. pucheranii* and *N. geoffroyi* probably are in broad contact in eastern Ecuador-Peru and western Brazil; nothing is known, however, on the interaction of these two species (see above under *N. geoffroyi*). The Venezuelan species *N. rufipennis* is separated by a distributional gap from *N. pucheranii*.

Discussion

Superspecies or species group? — The neotropical ground-cuckoos form a group of four closely related species which probably occupy a single ecological niche of a "large terrestrial and mainly insectivorous forest bird foraging around army ant swarms". They also eat lizards and probably other small animals. Ecological competition may lead to geogra-

¹) Peters (1940, p. 63) discussed the two cotypes of *N. pucheranii* in the Paris Museum on the basis of information supplied to him by C. E. Hellmayr in a letter dated September 9, 1936 (archives Mus. Comp. Zool., Harvard Univ., Cambridge; R. A. Paynter, pers. comm.). The specimen selected by Peters (1940) as the type of *N. p. pucheranii* is labelled "No. 1831. Pérou, Santa María ... ♂" (Hellmayr l.c.). Santa María de las Yaguas is situated in the forest interior to the north or northeast of Pebas and at some distance from the bank of the Amazon River: [Father Rosas] "était parvenu à réunir las Yaguas dans un établissement situé à deux jours de voyage dans intérieur" [from Pebas]; Castelnau "Histoire du Voyage", vol. 5, 1851, part I, p. 12. Further information is given on p. 24—25 of the same publication, where it is stated that the missionaries had changed the name "Saint-José" (= San José) to Santa María de las Yaguas. J. T. Zimmer located this village at "about 7155 0305 SA 19" (Vaurie 1972) which may be correct. Zimmer does not, however, give any reason for his selecting the above coordinates. Santa María may conceivably be located somewhat to the east of Zimmer's location in the headwater region of the Yaguas River which, northeast of Pebas, flows into the Rio Putumayo.

phical exclusion of ground-cuckoos in areas, where two species come in contact (upper Amazonia and possibly in western Colombia), even though conspicuous differences in plumage color and behavior(?) probably assure reproductive isolation. I assume that geographic exclusion without hybridization would result if Venezuelan *N. rufipennis* came in contact with Amazonian *N. pucheranii* and/or with *N. geoffroyi* which, therefore, are taxonomically ranked as species. I group the ground-cuckoos in two "zoogeographic species" (Mayr et al. 1970: 3), the *Neomorphus geoffroyi* superspecies and the *N. rufipennis* superspecies¹⁾. The four species occupy mutually exclusive geographical ranges and together form the *N. geoffroyi* species group²⁾. Other authors might prefer to combine all four species as one superspecies or to treat *N. radiolosus* and *N. geoffroyi* as taxonomically more isolated ("independent") species. No criterion (natural, artificial, operational or otherwise) exists to delimit the informal categories of "superspecies" and "species group", unless a rather extensive geographical overlap occurs in the species involved. The relative extent of overlap permitted for members of a superspecies is undefined (allospecies are "largely or entirely allopatric", Mayr 1969: 52; allospecies "meet parapatrically ... or even overlap slightly", Mayr et al. 1970: 100). In related allopatric species showing varying degrees of differentiation, it is similarly difficult to decide whether or not the superspecies has reached the level of a species group, i.e. whether or not the allospecies are potentially capable of invading one another's ranges to live sympatrically. In other words it is difficult "to know at what point in the evolution of a superspecies it is no longer useful to employ the term, even though the pattern of the species may still fall within the definition of 'mainly allopatric'" (Hall 1972).

A few examples from neotropical birds may illustrate these difficulties. The aracari-toucan *Pteroglossus aracari* is parapatric with *P. pluricinctus* in southern Venezuela and with *P. castanotis* in Brazil. Therefore, these three closely related species could be grouped as a superspecies. However, *P. pluricinctus* and *P. castanotis* are extensively sympatric in upper Amazonia (Haffer 1974: 225, Fig. 16.19), which could lead one to designate the three species as a species group. The barred woodpeckers *Celeus undatus* and *C. grammicus* form an Amazonian superspecies. The trans-Andean *C. loricatus* is allopatric and may or may not be sufficiently closely related to these two Amazonian species to be included in the *C. undatus* superspecies (Haffer 1974, Fig. 9.10). Six blue cotingas, viz. *Cotinga amabilis*, *ridgwayi*, *nattererii*, *cotinga*, *maculata*, and *maynana*, are either allopatric or parapatric. Whereas Snow (1973) grouped only the first three species as a superspecies, Haffer (1974, Fig. 9.2) included all six as members of one superspecies to emphasize the presumed common history of these closely related species. The members of the two subgroups *amabilis-ridgwayi-nattererii* and

¹⁾ A *superspecies* is a monophyletic group of entirely or essentially allopatric species that are too distinct to be included in a single species (Mayr 1963: 672).

²⁾ A *species group* is a group of closely related species, usually with partially overlapping ranges (Mayr 1963: 672).

Table 1: Color characters and measurements of
the neotropical Ground-Cuckoos, *Neomorphus geoffroyi* species group.

Species	Upperhead	Breast
<i>N. geoffroyi</i>		
<i>salvini</i> group	Forehead and crown uniform rufous (<i>N. g. salvini</i>) or brown (<i>N. g. aequatorialis</i>); crest blueblack.	Feathers tipped pale, dusky semicircular bands obscure; narrow pectoral band black.
<i>geoffroyi</i> group	Forehead and crown barred cinnamon-rufous and dark blue; crest dark blue.	Feathers with dusky semicircular bands; narrow pectoral band black.
<i>N. radiolosus</i>	Blueblack, forehead barred buffy white	Banded black and white; feathers with black semicircular bands; pectoral band indistinct.
<i>N. pucheranii</i>	Uniform dark blue	Ashy or buff; feathers faintly or boldly margined black; narrow pectoral band black.
<i>N. rufipennis</i>	Uniform blueblack	Blueblack or dark blue.

cotinga-maculata are closer to one another than to members of the other subgroup or to *C. maynana* and might conceivably still be conspecific (see also Snow 1973: 23—24). I here propose to group the six *Cotinga* forms as three species, viz. *C. nattererii* (incl. *amabilis* and *ridgwayi*), *C. cotinga* (inc. *maculata*), and *C. maynana*. The latter two species are in broad contact in upper Amazonia and intermediate specimens are unknown. A further example are the neotropical jays of the *Cyanocorax cayanus* group. Eight species are either allopatric or parapatric and have been grouped into three superspecies by Haffer (1975).

The processes which occur during the differentiation of a species into a superspecies and of a superspecies into a species group are as gradational as the transition of subspecies to species. Therefore, taxonomic treatment of transitional cases will remain subjective as long as no formal criteria for delimiting these evolutionary levels have been established (e. g. relative extent of geographical overlap permitted for allospecies; degree of

Table 1 (continued)

Bill	Feet	Iris	Orbital skin behind eye
Light horn, dull gray, green, olive gray.	Gray	Reddish brown, dark brown.	Neutral gray in adults and dark gray with bright blue spot in juveniles (<i>N. g. salvini</i>) or blue (<i>N. g. aequatorialis</i>).
Greenish yellow or light bluish green; tip pale.	Gray	Red, yellowish red, light red, or outer ring red and inner ring yellow. Brown, reddish brown (<i>N. g. australis</i>).	Blue
Blackish horn color, tip bluegray.	Olive gray, bluish gray.	Brown, red	Blue
Red, tip peagreen.	Horn- color	Brown	Red and posteriorly blue
Black, tip yellowish green.	Olive	Brown	Red

hybridization allowed for parapatric species)¹). This may be achieved when more examples of critical transitional levels will have been analysed in detail. It should be emphasized, however, that any species/subspecies limit agreed upon will fall in a continuum and will arbitrarily separate

¹) For example, Short (1969: 89) proposed as a convenient limit for species/subspecies the occurrence of both parental phenotypes in numbers of 5%, taken together, of the population in the 'zone of overlap and hybridization'. Difficulties of delimiting, even artificially, the species and subspecies category will remain in those rather rare cases where two forms hybridize extensively in some portions of the contact zone but remain parapatric or even overlap slightly without hybridization in other areas of contact such as, e.g., *Pipilo* forms in Mexico, Paradise Flycatchers in Africa, *Passer* and *Alectoris* forms in southern Europe (see summaries by Mayr 1963: 118—125 and, for *Alectoris*, by Glutz et al. 1973: 226).

some forms which are in reality more similar to each other than to many forms within their own respective categories. It goes without saying, of course, that neither of the terms "superspecies" and "species group" has nomenclatural standing or describes well delimited phenomena. Yet in view of their usefulness in designating evolutionary stages in the differentiation of a group of related species, these terms are justified, but their application requires standardization in order to assure effective communication.

The four ground-cuckoos are divided on the basis of several color characters into the following two groups (Table 1):

- A. *Neomorphus geoffroyi* and *N. radiolosus*: Color of upper head and crest not uniform; feathers of lateral breast with dusky or black semi-circular bands; orbital skin blue.
- B. *Neomorphus pucheranii* and *N. rufipennis*: Color of upper head and crest uniform blueblack; feathers of lateral breast gray or clay color margined apically faintly to broadly with black or blueblack; orbital skin red and blue or entirely red.

Member species of group A above probably are more closely related to each other than to members of group B and each group has an immediate ancestor (Fig. 3). For this reason I designate group A as the *Neomorphus geoffroyi* superspecies and group B as the *N. rufipennis* superspecies, combining both superspecies in the *N. geoffroyi* species group:

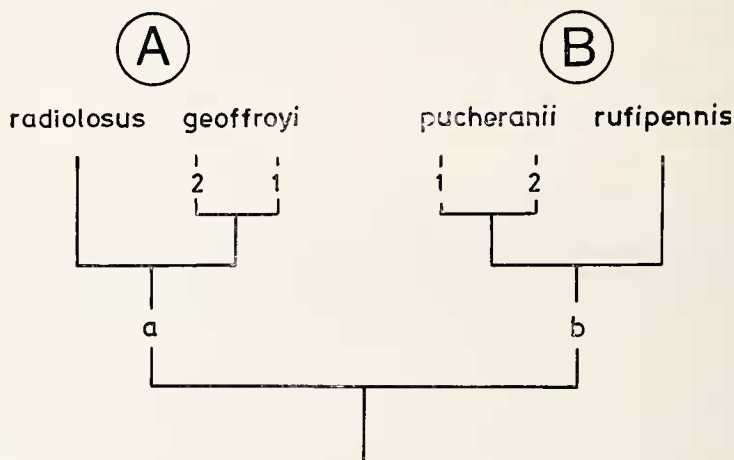


Fig. 3: Probable phylogenetic relationships of the neotropical ground-cuckoos, genus *Neomorphus*.

Explanations: A — *Neomorphus geoffroyi* superspecies. B — *Neomorphus rufipennis* superspecies. *Neomorphus radiolosus* and *N. rufipennis* are monotypic; *N. geoffroyi* consists of the *geoffroyi* (1) and *salvini* (2) subspecies groups. The species *N. pucheranii* comprises *N. p. pucheranii* (1) and *N. p. lepidophanes* (2).
a — proto- [*geoffroyi*], b — proto- [*rufipennis*].

Table 2: Measurements of the neotropical ground-cuckoos,
Neomorphus geoffroyi species group

Species	Locality	Measurements (mm)			
		Wing (flat)	Tail	Bill from nostril	
<i>N. geoffroyi</i> superspecies	<i>N. geoffroyi</i>				
	<i>salvini</i> group	Middle America, <i>N. g. salvini</i> , 5 ♂ (Ridgway 1916);	167—178 (172.8)	258—271 (261.8)	—
		6 ♂ (Wetmore 1968);	165—175 (169.3)	244—262 (254.8)	
		San José de Sumarco, Ecuador, <i>N. g. aequatorialis</i> , 2 ♂.	166, 168	—	33.3, 32.6
	<i>geoffroyi</i> group	Baião, Rio Tocantins (<i>N. g. geoffroyi</i>), 2 ♂.	159, 160	264, 259	31.9, 29.7
		Maruins, Rio Machados, Brazil, 1 ♂.	173	254	32
		Baixo Guandú, Espírito Santo (<i>N. g. dulcis</i>) 2 ♂.	172, 174	275, 274	31.4, 33.5
		Rio São José, Espiritu Santo (<i>N. g. dulcis</i>) 1 ♂.	171	273	31.5
		Parintins (<i>N. g. squamiger</i>) 1 ♂.	162	246	31
		Huacamayo, Perú, 1 ♂ (<i>N. g. australis</i>)	162	—	31.1
<i>N. rufipennis</i> superspecies	<i>N. radiolus</i>	Paramba, NW Ecuador, 2 ♂.	162, 168	230, 232	33.3
	<i>N. pucheranii</i>	Orosa and San Fernando, Perú, 3 ♂ (<i>N. p. lepidophanes</i>)	172, 176, 180	263, 269	35.2, 35.5, 36
	<i>N. rufipennis</i>	Mt. Auyántepeui and Suapure, Venezuela, 2 ♂	170, 175	281, 268	35, 32.8

*Neomorphus [geoffroyi]*¹⁾ *geoffroyi* (Temminck, 1820)

Neomorphus [geoffroyi] radiolosus Sclater & Salvin, 1878

Neomorphus [rufipennis] rufipennis (G. R. Gray, 1849)

Neomorphus [rufipennis] pucheranii (Deville, 1851)

Other authors might propose to unite all four species as one super-species, since the ground-cuckoos are relatively close in coloration and still unable to overlap their ranges. However, more than one immediate ancestor probably is involved which induces me to accept two superspecies despite the fact that all four species of ground-cuckoos still exclude each other geographically. It may be advisable to broaden the term "zoogeographic species" to include not only "independent" species without close relatives and superspecies as originally proposed by Mayr et al. (1970) but also those species groups whose member species do not (yet) overlap geographically. If this is done, the two *Neomorphus*-superspecies together could be considered as one zoogeographic species.

Comparison with other avian superspecies in Amazonia. — Many neotropical birds are members of superspecies, e. g. 76 % of the jacamars, 85 % of the toucans and 75 % of the cracids (Haffer 1974: 170). Vuilleumier (1972) found that, on the average, 53 % of the species in his sample of South American birds are allospecies of superspecies. In comparing the distribution pattern of the ground-cuckoos with that of other avian superspecies and species groups we notice similarities and differences. The occurrence of species with a restricted range in Pacific Colombia-Ecuador and in the highlands of southern Venezuela-Guyana is a common feature as is the widespread occurrence of clinally varying populations in southern Amazonia and in southeastern Brazil.

The distribution of ground-cuckoos in upper Amazonia is unusual, as one species (*Neomorphus pucheranii*) inhabits the lowlands and another one (*N. geoffroyi aequatorialis*) the Andean foothill zone. This situation compares somewhat with the distribution of members of the *Pipra serena* superspecies: *P. coronata* in the lowlands, *P. isidorei* in the Andean foothills; and of members of the *Galbula galbula* superspecies: *G. tombacea* — *G. cyanescens* in the lowlands and *G. pastazae* in the lower montane zone (see Haffer 1970: 312; 1974: 333). There are many species pairs in upper Amazonia, members of which replace each other in a north-south direction, i. e. from eastern Ecuador to eastern Perú (Haffer 1974: 57 and 99). In these cases, the Andean foothill zone and the eastwardly adjoining lowlands in Ecuador (north) and in eastern Perú (south), respectively, are inhabited by the same species. It would be interesting to discover if additional avian

¹⁾ The superspecific name, which is also the oldest specific name in the group, is enclosed in square brackets following a recommendation by Amadon (1966, 1968).

superspecies in upper Amazonia have distribution patterns similar to those of the ground-cuckoos *N. pucheranii* and *N. geoffroyi* as well as the pipras and jacamars mentioned above.

The close relationship of the cuckoo population in the Andean foothill zone (*N. geoffroyi aequatorialis*) with that of Middle America (*N. g. salvini*) is another characteristic feature in the distribution of the *N. geoffroyi* species group.

Historical interpretation. — The component species (allo-species) of avian superspecies in the forested neotropical lowlands probably originated from an ancestor whose range was repeatedly fragmented through vegetational changes during adverse climatic periods, i. e. during Pleistocene and post-Pleistocene arid phases (Haffer 1967, 1969, 1974). "Sister" populations inhabiting isolated remnants of the forest ("refuge" areas) during such periods deviated at varying rates from their ancestor, and from each other, by selection, chance and the varying "plasticity" of systematic groups. Upon return of more favorable climatic and vegetational conditions, newly developed forms came into secondary contact with varying results, according to the stage reached in the speciation process, viz., more or less extensive hybridization, geographical exclusion or range overlap of varying extent. Zones of secondary contact between Amazonian forest birds reveal striking faunal discontinuities in a continuous forest environment.

The above historic interpretation of faunal differentiation in the Neotropical Region was recently supported by herpetological (Vanzolini 1970, 1973, Vanzolini et al. 1970), phytogeographical (Prance 1973) and general zoogeographical studies (Müller 1973) in Amazonia. Brown et al. (1974) and Brown (1975) analysed the geographical patterns of evolution in *Heliconius* butterflies and reconstructed the probable location of forest refugia of importance for the speciation in these insects. The results largely agree with those of previous authors indicating that the principal centers of differentiation for the neotropical forest fauna have likely been identified. A larger number of forest refugia have been postulated for butterflies than for birds, which suggests, as might be expected, that insects survived more readily than birds in small forest remnants.

We may speculate that during an early Pleistocene arid climatic phase, the range of the ancestor of the *N. geoffroyi* species group was divided into two isolated regions, to the north (proto-*rufipennis*) and to the south (proto-*geoffroyi*) of the Amazon River. Upon invasion of the Pacific lowlands of Colombia and northwestern Ecuador by proto-*geoffroyi*, *N. radiolosus* branched off as a heavily pigmented isolate of the excessively

humid Chocó region. On the other hand, proto-*rufipennis* may have given rise to *N. pucheranii* and *N. rufipennis* in late Pleistocene forest refugia of their respective distribution areas (Napo and Tepui refuges). These phylogenetic relationships are illustrated diagrammatically in Figure 3.

The separation between the upper Amazonian Napo refuge and the Abitagua refuge in the foothills of the Ecuadorian mountains is an interesting aspect of Brown's (1975) map of the Pleistocene forest refugia in the Neotropics. I would assume that the Redbilled Ground-Cuckoo (*N. pucheranii*) originated in the lowland forests of the Napo refuge, and the *salvini* group of *N. geoffroyi* in the Abitagua refuge of the Ecuadorian foothills, the latter form probably together with *Galbula pastazae* (Haffer 1974: 341), *Pipra isidorei* (Haffer 1970: 315) and other submontane bird species.

The early representative of the *salvini* subspecies group of *N. geoffroyi* may have reached Central America from eastern Ecuador via the Magdalena Valley (M of Fig. 1) and the northern tip of the Central Andes of Colombia rather than by following the Eastern Andes into northwestern Venezuela and northeastern Colombia. After the trans-Andean population was isolated from the eastern Ecuadorean "parent" population, they were differentiated as *N. g. salvini* (Caribbean Costa Rica refuge) and *N. g. aequatorialis* (Abitagua refuge), respectively. *N. g. salvini* later reached Nicaragua and (re)invaded northwestern Colombia but was unable to enter western Colombia which was previously occupied by the earlier trans-Andean isolate *N. radiolus*.

The ancestor of the *geoffroyi* group of the Rufous-vented Ground-Cuckoo may have originated in the Belém refuge, south of the mouth of the Amazon, reaching southeastern Brazil when improved forest connections permitted the extension of the range, and also spreading westward to the Andes of southeastern Perú and Bolivia (*N. g. australis*). It is not known whether contact with the *salvini* group, i. e., *N. g. aequatorialis*, was established in southeastern Perú. The geographical variation of the *geoffroyi* group in the vast forests of southern Amazonia and southeastern Brazil is mostly clinal, although *N. g. squamiger* may have originated in an isolated forest refuge. However, more data and specimens are needed from central Brazil for a study of the history of the ground-cuckoos occupying this area today.

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Summary

The neotropical ground-cuckoos (*Neomorphus*) are pheasant-like terrestrial birds with long tail, strong legs and a flat crest. They catch insects at army ant swarms in the forest interior from Nicaragua through Amazonia to southeastern Brazil. Ground-cuckoos inhabit the forest floor in well-drained hilly terrain and as swift runners are difficult to collect.

Four species of ground-cuckoos replace each other geographically and form two superspecies as follows: *Neomorphus geoffroyi* superspecies (*N. geoffroyi*, *N. radiolosus*) and *N. rufipennis* superspecies (*N. rufipennis*, *N. pucheranii*). The geographically restricted species *N. radiolosus* and *N. rufipennis* are monotypic. *N. pucheranii* consists of two subspecies separated by the Solimões River. *N. geoffroyi* is composed of two subspecies groups, the *N. g. geoffroyi* group with 5 subspecies (including *N. g. squamiger*) and the *N. g. salvini* group with 2 subspecies. Both groups may or may not be in contact in eastern Perú. Nothing is known on the interrelationship of *N. geoffroyi* and *N. pucheranii* along their presumed extensive contact zone in eastern Ecuador, northeastern Perú and western Brazil. The broad lower Amazon River prevents the northward dispersal of *N. geoffroyi*, which remains widely separated from southern Venezuelan *N. rufipennis*.

As in other avian superspecies of the neotropical lowlands, the four species of ground-cuckoos probably originated from an ancestor, whose range was repeatedly fragmented through vegetational changes during adverse climatic periods of the Quaternary. Speciation occurred in small remnant populations isolated in refuge forests.

Zusammenfassung

Systematische Übersicht der neotropischen Bodenkuckucke (Aves, Neomorphus). — Die Bodenkuckucke Mittel- und Südamerikas sind fasanenähnliche terrestrische Vögel mit langem Schwanz, kräftigen Beinen und flacher Haube. Sie bewohnen den Boden hügeligen Waldlandes und sind als schnelle Laufvögel schwer zu jagen. Ihr Nest steht wahrscheinlich im dichten Unterwuchs des Waldes. Das Verbreitungsgebiet der Bodenkuckucke erstreckt sich von Nicaragua durch Amazonien nach Südost-Brasilien.

Vier *Neomorphus*-Arten vertreten einander geographisch und bilden zwei Superspezies: Superspezies *Neomorphus geoffroyi* (*N. geoffroyi*, *N. radiolosus*) und Superspezies *N. rufipennis* (*N. rufipennis*, *N. pucheranii*). Während *N. radiolosus* und

N. rufipennis monotypische Arten sind, werden bei *N. pucheranii* 2 Subspezies unterschieden, deren Verbreitungsgebiete der Rio Solimões trennt. *N. geoffroyi* besteht aus 2 Subspezies-Gruppen. Über das gegenseitige Verhalten von *N. geoffroyi* und *N. pucheranii* entlang einer vermuteten Kontaktzone in Ost-Ecuador, Ost-Perú und West-Brasilien ist nichts bekannt. Der breite untere Rio Amazonas verhindert eine nördliche Ausbreitung von *N. geoffroyi*. Diese Art ist daher weit getrennt von *N. rufipennis* aus dem Bergland von Süd-Venezuela und Guyana.

Wie bei zahlreichen anderen Superspezies der neotropischen Tiefländer stammen die Arten der südamerikanischen Bodenkuckucke wahrscheinlich von einem Vorfahren aus dem Amazonas-Walde ab, dessen Verbreitungsgebiet während arider Klimaperioden des Quartärs durch Veränderung der Vegetationsdecke wiederholt in mehrere Teile zerlegt wurde. Die Splitter-Populationen entwickelten sich in der Isolation zu unterschiedlichen Arten.

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